Indian Phytopath. 60 (1) : 13-23 (2007)

Genetic resistance to foliar anthracnose in sorghum and pathogenic variability in *Colletotrichum graminicola*

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ABSTRACT: Anthracnose, caused by the fungus *Colletotrichum graminicola*, is a widely prevalent and economically significant disease of sorghum (*Sorghum bicolor*) in warm and humid regions of Asia, Africa and the America. Disease management through host plant resistance is the most effective option, but the resistance has been often short-lived because of the highly variable pathogen forms. Resistance to foliar anthracnose in sorghum lines and variability in *C. graminicola* populations were studied through a collaborative International Sorghum Anthracnose Virulence Nursery (ISAVN). The ISAVN, consisting of 15 sorghum lines, were tested at 14 anthracnose hot spots in India, Thailand, Ethiopia, Kenya, Zambia, Nigeria and Mali for 4-7 years (1992-1998). Foliar anthracnose severity data were recorded at the hard-dough stage of the crop. Anthracnose severity varied significantly among lines, years and locations. The tested sorghum lines exhibited significantly differential resistance. Among the 15 sorghum lines IS 6928, IS 18758, and IS 12467 were the most resistant to anthracnose across the environments (locations and years). Analysis of variation in anthracnose severity revealed that resistance in sorghum lines was variable and dependent on the environment, indicating potential differences in virulence of *C. graminicola* populations at different locations and over years. Correlation and cluster analyses based on the reactions of tested sorghum lines at different locations suggested that some of the sorghum lines may share certain resistance genes and that the two most resistant lines IS 12467 and IS 6928, may possess different resistance genes. These lines could be ideal sources of resistance for breeding programs.

Key words: Sorghum, anthracnose, stable resistance, pathogenic variation

Anthracnose of sorghum (*Sorghum bicolor* L.), caused by *Colletotrichum graminicola* (Ces.) Wilson is an important and widespread disease worldwide. The pathogen infects stalks, foliage, peduncles and panicles causing substantial loss to both grain and forage production (Ali and Warren, 1992; Thakur and Mathur, 2000; Mathur *et al.*, 2002). Among these, foliar infection is the most pronounced and devastating on the forage and grain sorghum cultivars (Casela and Frederiksen, 1995). Host plant resistance, as a strategy to control this disease, has often failed because of the extensive genetic variation in pathogen populations. A number of resistance sources are available and several have been used to produce commercial hybrids in the United States and India (Boora *et al.*, 1998; Thakur,

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1995; Thakur *et al.*, 1997). However, resistance durability in these cultivars has short-lived because of evolution of cultivar-specific virulence in the pathogen population (Casela *et al.*, 1998; Rosewich *et al.*, 1998; Rao *et al.*, 1998; Thakur and Mathur, 2000). Evidence for dilatory resistance (resistance expressed at late crop growth stage) in sorghum lines against *C. graminicola* has also been reported (Casela and Frederiksen, 1995). More than 40 races/pathotypes have been reported from different geographical areas of the world, using different sets of putative host differentials (Pande *et al.*, 1991; Thakur *et al.*, 1998; Marley *et al.*, 2001, 2004; Mathur *et al.*, 2002; Rooney *et al.*, 2002; Casela and Ferreira, 1995). Since the first report of existence of races in *C. graminicola* in the United States in 1967 (Harris and Johnson, 1967), 11 races/ pathotypes have been reported from the US and Puerto-Rico (Ali and Warren, 1987; Cardwell *et al.*, 1989); 12 from Brazil (Ferreira and Casela, 1986); 9 from India (Pande *et al.*, 1991); 15 from Nigeria (Ozuloa *et al.*, 1986; Marley *et al.*, 2001; 2004), and 2 from western Africa (Neya and Normad, 1998; Thomas, 1995). However, the actual number of races/pathotypes and their genetic variability at the global level are unclear as no clear gene-for-gene relationship has been established for any host-isolate systems. In order to develop effective strategies for management of this disease through host resistance, it is important to obtain information on pathogenic variability and resistance stability. With this objective in mind a collaborative International Sorghum Anthracnose Virulence Nursery (ISAVN) was established in 1992 to identify sorghum lines with stable resistance to anthracnose and understanding pathogenic variability in *C. graminicola* populations at select "hot-spots" (where disease occurs regularly every year) in major sorghum growing areas of the world. The nursery comprised of sorghum lines that had shown differential reactions in earlier tests. The International Crops Research Institute for the Semi-Arid Tropics, (ICRISAT) Patancheru, India, coordinated the ISAVN from 1992 through 1998. The results of 4-7 years of ISAVN conducted at 14 locations in seven countries in Asia and Africa are reported and the implications of these results in managing the sorghum anthracnose through host plant resistance are discussed.

MATERIALS AND METHODS

Sorghum lines and nursery locations: A set of 15 sorghum inbred lines belonging to different races of cultivated sorghum from different geographic origins having variable agronomic traits were used (Table 1) in this study. These lines were selected on the basis of their differential reactions to anthracnose in several field and greenhouse tests (Pande *et al.*, 1994). Seed stocks of these 15 lines were increased and maintained at ICRISAT, Patancheru and sub-sampled for supplying to the collaborators. In addition at each location, a local resistant line and a local susceptible line were included as controls (although these lines were not the same each year at each location) making the total number of lines to 17. The locations were selected from known anthracnose "hot spots" in several countries. A total of 14 locations, seven in India, two in Mali, and one each in Thailand, Ethiopia, Zambia, Kenya and Nigeria were selected to represent a wide range of geographical diversity

Table 1. Sorghum lines, their cultivated races and origins used in the International Sorghum Anthracnose Virulence Nursery (ISAVN) 1992-1998

Sorghum line[a]	Race of cultivated sorghum	Country of origin
IS 8354	Caudatum bicolor	USA
IS 3758	Caudatum bicolor	Ethiopia
IS 3552	Caudatum	Sudan
IS 2508 (MN 760)	Kafir caudatum	USA
IS 36563	Durra caudatum	Niger
IS 6928	Kafir caudatum	Sudan
IS 854 (FC 11531)	Kafir caudatum	USA
IS 1006 (SA 6480)	Kafir bicolor	India
IS 6958	Durra caudatum	Sudan
IS 12467	Caudatum	Sudan
IS 17141 (N 565)	Durra caudatum	Nigeria
IS 18758 (ET 35-1)	Guinea caudatum	Ethiopia
IS 18760 (1609B)	Durra kafir	USA
[b]ICSV 247	Caudatum	India
IS 18442 (H 112)	Guinea durra	India
IS 3089 (S)	Bicolor	USA

[a]IS = International Sorghum accession number assigned at ICRISAT's genebank; alternate identity in parenthesis.

[b]ICSV = ICRISAT Sorghum Variety.

(latitude 0.31 to 29.05 °N; longitude 5.39 to 100.4 °E; annual rainfall 627 to 2614 mm). Weather data, particularly of temperature (Tmin and Tmax) and relative humidity (RHmin and RHmax) were recorded at 13 of the 14 locations for 60 days, from 30-day (pre-boot stage) to 90-day (hard-dough stage) of the crop growth. The average Tmin varied from 14-16°C at Bako and Alupe to 24-26°C at Surat; Tmax varied from 23-27°C at Bako to 32-37°C at Samanko; average RHmin varied from 15-62% at Bagauda to 69-82% at Dharwad, and RHmax from 55-90% at Bagauda to 94-100% at Bako (Table 2). At each of these locations the trial was conducted for 4 to 7 years.

Nursery management: The trial was established at each location during the rainy seasons to provide congenial conditions for anthracnose development. The nursery was laid out in a randomized complete block design with two replications. Each plot comprised of two rows of 4 m length. Ten days after emergence, plants were thinned to maintain 20-25 plants per row. General agronomic practices were followed at each location to raise the sorghum crop and the crop was protected from insect pests by the application of insecticides. At most locations weather conditions were congenial for anthracnose development. However, at certain locations in some years (Patancheru 1994, 1996; Dharwad 1993, 1997; Udaipur 1996, 1998) when weather was not congenial 30-day-old plants were artificially inoculated and high humidity was provided by sprinkler irrigation to obtain a reasonable level of disease pressure.

Data collection and analysis: At the soft-dough stage, 10 uniformly growing plants from each of the two rows were tagged and at the hard-dough stage (about a week later) the top four leaves were scored for disease severity as percentage leaf area covered by anthracnose lesions. The mean disease severity for each plant was calculated from the scores of the four leaves. Because the local resistant and susceptible control lines were different at each location, they were not included in some of the analyses. Mixed model procedure (SAS, 9.1 release, SAS Institute Inc., Cary, NC 27513, USA) in which replication, replication × year and replication × year × location were considered random effects was used to perform analysis of variance to determine the effects of sorghum line, geographical location, year, and their interactions (fixed effects) on anthracnose severity. The percentages of tests in which a sorghum line showed high resistance (<10% of leaf areas on the

Table 2. Weather variables at test locations of International Sorghum Anthracnose Virulence Nursery, 1992-98

Country	Location	Latitute (°N)	Longitude (°E)	Years of testing	Mean rainfall (mm)	Weather variables during the trial season[a]			
						Tmin (°C)	Tmax (°C)	RHmin (%)	RHmax (%)
India	Dharwad	15.47	75.02	4	814	19-21	27-29	69-82	91-92
	Indore	22.72	75.83	7	935	22-24	29-30	-[b]	82-88
	Kovilpatti	9.17	77.87	5	736	17-22	30-31	66-75	93-94
	Pantnagar	29.05	79.52	6	2614	21-24	31-33	59-72	89-95
	Patancheru	17.53	78.27	7	890	21-23	29-31	67-72	88-93
	Surat	20.97	72.90	7	1070	24-26	27-34	51-76	75-84
	Udaipur	24.58	73.68	7	627	19-23	28-31	52-75	80-92
Thailand	Bangkok	13.68	100.40	5	-[b]	21-25	31-32	52-63	84-94
Ethiopia	Bako	9.1	37.15	5	1170	14-16	23-27	53-72	94-100
Kenya	Alupe	0.31	38.04	6	1100	14-16	30-31	56-59	77-83
Zambia	Mansa	11.1	28.8	4	1177	-[b]	-[b]	-[b]	-[b]
Mali	Longorola	11.23	5.39	4	1000	22-23	27-31	58-59	94-95
	Samanko	12.32	8.05	7	-[b]	20-23	32-37	63-76	87-91
Nigeria	Bagauda	11.01	11.28	4	846	21-22	31-32	15-62	55-90

[a]Mean of 60-day data from 30-day (pre-boot stage) to disease scoring at the hard-dough stage of the crop.
[b]Data not available.

top four leaves covered by anthracnose lesions with little or no sporulation- spores and setae) and high susceptibility (>40% of leaf areas on the top four leaves covered by anthracnose lesions with abundant sporulation) were calculated to estimate the probabilities of a certain sorghum line showing a resistance and susceptible reaction, respectively. Then the probabilities of different lines were used as an indicator of resistance stability.

A correlation analysis (CORR procedure, SAS 9.1 release) was performed on anthracnose severity between different lines to determine the association between lines in the reaction to *C. graminicola* populations. Cluster analysis (SAS Version 9.1, SAS Institute Inc., Cary, NC27513) was also performed to group the 15 tested sorghum lines based on their reaction to anthracnose pathogen across geographical locations and years.

RESULTS

Reaction of sorghum lines to anthracnose at different locations: The average anthracnose severity on the 15 test lines across locations/ environments was generally low to moderate, but varied widely with leaf areas covered by lesions ranging from 0 (at Indore) to 80.7% (at Bagauda) (Table 3). Similarly, the average anthracnose severity on local resistant sorghum lines varied from 0 (at Bangkok) to 18.5% (at Mansa) and those on local susceptible lines from 5.3% (at Bangkok) to 59.3% (at Indore). Variance analysis for the 15 test lines revealed that the effects of location, year, line, and interactions between them were all significant ($P \leq 0.0001$) (Table 4). Of the 15 test lines, IS 6928 (Kafir caudatum from Sudan), IS 18758 (Guinea caudatum from Ethiopia), and IS 12467 (Caudatum from Sudan) were more resistant with anthracnose severity ranging from 9.1 to 10.5% than other lines, such as IS 3089 (S), IS 1006, and IS 3758, with severity ranging from 20.4 to 48.9%. Two test lines IS 12467 and IS 6928 although had mean anthracnose severity of 10.1 and 9.5%, respectively their responses to anthracnose infection at different locations varied from 1.2% (at Alupe) to 31.9% (at Pantnagar) for IS 12467, and 0.0 % (at Bangkok) to 22.2% (at Bako) for IS 6928 (Table 3). Similarly, although IS 1006 was generally highly susceptible to anthracnose, it had consistently exhibited resistance at Dharwad, Indore, and Alupe. Among 154-160 tests (4-7 years × 14 locations × 2 replications), some lines exhibited higher stability of resistance than others (Table 5). For example, IS 17141 and IS 2508 although showed similar mean disease severity (16.8 and 14.2%), IS 2508 was much more stable with resistance being expressed in 58% of tests than IS 17141 that expressed resistance in 53% of the tests.

Correlation between anthracnose severities of sorghum lines: Anthracnose severity on some tested sorghum lines was significantly correlated with each other over the locations and years (Table 6). For instance, anthracnose severity on IS 8354 was positively correlated with those on IS 3758 (r = 0.64), IS 2508 (r = 0.62), IS 1006 (r = 0.56), IS 12467 (r = 0.52), and IS 18760 (r = 0.54). Similarly, anthracnose severity on IS 6928 was positively correlated with those on IS 36563 (r = 0.41), IS 6958 (r = 0.41), IS 18758 (r = 0.45), and ICSV 247-R (r = 0.54).

Similarity among sorghum lines for anthracnose resistance: Cluster analysis based on the anthracnose severity at different geographical locations and years successfully identified relationship among the 15 tested sorghum lines (Fig. 1). Some sorghum lines that showed similar anthracnose reactions across different locations and years were grouped closely, while those exhibiting unique reactions were grouped separately. Sorghum line IS 8354 was closer to IS 3758 than to any other lines, therefore the two were classified into Group I. IS 3552, IS 2508, IS 18760, IS 17141, IS 854, and IS 12467 were all similar and formed Group II, while IS 6928, ICSV 247-R, IS 18758, and IS 6958 were grouped together in Group III with IS 36563 (in group V) loosely related to this group, but distant from any other groups. Both IS 1006 and IS 3089 (S) were highly susceptible but varied differently across different geographical locations and were thus classified into two groups, group IV and VI, respectively.

DISCUSSION

In this study, we have demonstrated the variability of resistance in the tested sorghum lines against anthracnose among different geographical locations and identified lines with stable resistance at multiple locations. The results also indicated the

Table 3. Average percent leaf area covered by anthracnose lesions on the 15 tested sorghum lines at 14 locations in Asia, southern and eastern Africa (SEA) and western and central Africa (WCA) during 1992-98 (means are followed by standard deviations in smaller font directly beneath them)

Sorghum lines	Asia[a]								SEA[a]			WCA[a]		
	DWD (4yr [b])	IND (7yr)	KOV (5yr)	PAN (6yr)	PAT (7yr)	SUR (7yr)	UDR (7yr)	BAN (5yr)	BAK (5yr)	ALU (6yr)	MAN (4yr)	BAG (4yr)	LON (4yr)	SAK (7yr)
IS 8354	5.6	0.0	14.2	53.4	32.3	21.6	7.2	6.0	29.0	10.7	50.0	27.5	19.4	2.5
	7.9	0.0	21.0	23.8	14.8	10.7	5.4	9.8	25.4	16.1	28.4	13.3	27.4	4.2
IS 3758	11.0	1.5	13.6	51.3	20.0	27.4	10.8	19.5	35.5	32.5	27.8	29.5	4.6	2.0
	14.8	5.7	15.4	24.8	12.2	17.0	14.5	27.0	22.6	28.4	23.9	26.4	3.7	1.5
IS 3552	5.1	6.1	17.1	36.9	16.1	24.7	26.2	7.5	17.4	1.8	6.4	16.5	1.3	2.1
	4.4	15.7	13.5	23.8	9.8	10.4	20.2	8.7	19.6	3.0	8.6	10.5	1.5	2.7
IS 2508	5.0	3.5	12.2	39.8	17.8	28.1	14.1	5.1	14.7	0.2	17.8	18.6	7.4	8.1
	4.2	8.2	14.9	25.9	12.7	10.2	12.3	9.0	15.8	0.4	27.2	9.5	4.1	11.2
IS 36563	15.3	2.6	6.5	47.9	3.8	4.2	4.3	6.7	7.4	31.7	27.0	15.3	49.3	33.2
	21.6	6.4	10.0	19.9	2.4	1.5	4.6	17.8	15.6	24.2	18.6	8.7	32.0	27.2
IS 6928	4.5	0.2	3.3	12.4	2.4	4.7	8.6	0.0	22.2	15.8	17.6	3.1	21.2	17.1
	6.3	0.9	4.7	13.3	0.9	2.2	9.4	0.1	25.9	12.6	16.3	4.6	22.0	14.4
IS 854	5.7	4.4	12.9	29.7	24.5	16.1	17.3	1.2	13.4	0.5	19.4	35.7	2.8	4.7
	10.3	8.7	9.9	32.2	16.7	9.1	20.6	2.5	13.7	1.2	21.2	31.9	2.3	7.5
IS 1006	9.9	0.0	24.8	40.8	23.1	31.3	17.5	22.5	31.4	10.5	53.8	50.9	34.3	26.7
	11.0	0.0	19.6	25.2	19.9	13.0	19.1	28.6	18.7	14.4	29.4	33.1	25.2	24.5
IS 6958	3.3	6.5	6.4	11.9	3.2	6.4	8.0	1.2	13.9	31.4	50.3	10.4	4.7	19.0
	2.3	10.9	10.4	7.8	2.7	2.6	13.2	2.5	15.1	24.1	25.3	18.0	5.7	22.3
IS 12467	7.1	2.6	7.9	31.9	15.1	14.6	14.3	4.5	9.6	1.2	9.9	17.8	2.9	2.1
	12.9	6.1	9.5	30.1	13.0	7.2	15.1	12.0	8.1	3.1	15.0	16.4	3.1	2.7
IS 17141	5.1	1.4	15.7	37.6	13.7	34.1	9.8	13.1	18.5	0.3	20.5	30.0	12.8	19.3
	3.0	3.4	21.1	28.8	9.3	15.4	9.0	15.4	17.6	0.6	12.9	17.6	6.2	18.7
IS 18758	16.5	15.5	7.9	13.6	3.5	4.1	2.6	0.0	9.1	13.5	15.5	7.6	22.1	13.7
	23.7	25.0	11.5	19.3	1.4	1.6	1.6	0.0	8.9	17.0	18.6	12.2	25.3	11.0
IS 18760	3.3	3.7	11.0	33.4	16.9	21.9	17.7	8.1	13.5	3.4	4.9	22.1	1.5	1.3
	1.3	6.7	15.9	28.1	8.9	12.0	12.6	11.4	10.8	6.3	4.3	16.0	1.6	2.2
ICSV 247-R	9.9	0.7	5.2	12.0	4.8	4.9	5.0	0.3	11.6	36.9	39.2	4.9	37.8	20.8
	10.5	2.7	8.2	9.0	5.5	2.6	4.6	1.0	10.6	19.2	26.6	9.6	22.7	17.1
IS 3089-S	21.2	24.7	38.3	64.5	53.2	37.1	55.9	26.1	44.4	36.7	58.2	80.7	61.2	72.9
	14.7	22.7	24.8	27.0	17.2	18.9	14.6	13.4	34.7	36.2	34.9	11.7	32.1	26.7
Loc. Susc.	40.4	59.3	29.6	52.7	46.2	18.1	59.0	5.3	35.4	34.5	32.4	35.0	41.7	49.1
	31.1	25.1	32.4	26.7	33.9	9.8	17.9	8.6	34.5	26.7	18.5	19.3	35.2	31.3
Loc. Res.	6.1	0.2	7.2	6.3	5.6	6.6	2.1	0.0	10.5	7.9	18.5	3.3	0.9	1.3
	7.5	0.5	10.2	2.9	5.2	8.6	1.9	0.0	13.1	6.9	19.7	2.5	1.4	1.5

[a]DWD = Dharwad; IND = Indore; KOV = Kovilpatti; PAN = Pantnagar; PAT = Patancheru; SUR = Surat; UDR = Udaipur; BAN = Bangkok; BAK = Bako; ALU = Alupe (only long seasons in a year included); MAN = Mansa; BAG = Bagauda; LON = Longorola; SAK = Samanko. [b]Number of years in which data were used for analysis.

Table 4. Variance analysis on effects of year, location, line and their interactions on percent leaf area infected by anthracnose

Source	Df	Den Df	Type III SS	F Value	Pr.>F
Year	6	75.4	16387	24.65	<0.0001
Location	13	75.5	145545	100.68	<0.0001
Year × Location	60	75.3	141479	21.40	<0.0001
Line	14	1105	197048	266.99	<0.0001
Year × Line	84	1105	32771	7.39	<0.0001
Location × Line	182	1104	218071	22.67	<0.0001
Year × Location × Line	836	1104	290492	6.58	<0.0001

Table 5. Performance of the 15 tested sorghum lines across different years and locations

Sorghum lines	N[a]	Mean[b]	Std. Dev.[c]	Dis≤10%[d]	Dis≥40%[d]
IS 3089 (S)	154	48.88	29.14	12%	59%
IS 1006	160	26.10	25.02	36%	28%
IS 3758	159	20.35	22.82	53%	21%
IS 8354	160	19.25	22.34	49%	19%
IS 36563	159	17.27	22.57	60%	18%
IS 17141	160	16.82	18.33	53%	14%
IS 2508	160	14.18	16.65	58%	6%
IS 3552	160	13.97	16.44	55%	9%
IS 854	159	13.88	19.36	60%	11%
ICSV 247-R	159	12.69	17.33	65%	11%
IS 18760	160	12.31	15.16	59%	8%
IS 6958	160	12.06	17.84	68%	8%
IS 12467	160	10.46	14.99	68%	6%
IS 18758	158	9.96	15.32	75%	8%
IS 6928	157	9.14	13.43	74%	6%

[a]Number of tests = 4-7 years × 14 locations × 2 replications.

[b]Mean percentage of infected leaf area during the 1992-1998 trials across different locations.

[c]Standard deviation of the percentage.

[d]Percentage of tests (year × location × replication) in which the tested line was and highly resistant (no more than 10% lesion area), and susceptible (lesion areas > 40% leaf area) respectively.

existence of variable pathogen populations at different locations with different virulence levels. The limitation for screening resistance in sorghum against *C. graminicola* has been the lack of well-defined host differentials. Because of the highly variable nature of *C. graminicola* populations, defining the standard gene-for gene relationship between resistance and virulence in the sorghum-*C. graminicola* system has been difficult. However, there are sorghum inbred lines that serve as putative differentials to discern the virulence patterns in *C. graminicola* populations to a reasonable level (Thakur, 1995; Thakur and Rao, 1998). In the present study, 15 sorghum inbred lines, evaluated in nearly 80 environments (location × year), provided differential reactions, and the anthracnose severity on these lines varied greatly across different geographical locations and over years. Differential reactions of the sorghum lines to anthracnose require not only differential resistance among these lines, but also differential virulence in pathogen population. The significant effects of interactions between sorghum line and location, and between line and year suggested that the tested lines

Table 6. Pearson correlation coefficients between anthracnose severities on the tested sorghum lines during 1992-1998

Sorghum lines	IS 8354	IS 3758	IS 3552	IS 2508	IS 36563	IS 6928	IS 854	IS 1006	IS 6958	IS 12467	IS 17141	IS 18758	IS 18760	ICSV 247-R (S)	IS 3089
IS 8354	1.00	0.64*	0.42*	0.62*	0.38*	0.27	0.46*	0.56*	0.28	0.52*	0.50*	0.30	0.54*	0.33*	0.33*
IS 3758		1.00	0.37*	0.41*	0.31*	0.14	0.35*	0.42*	0.29	0.48*	0.43*	0.22	0.43*	0.30*	0.13
IS 3552			1.00	0.57*	0.05	-0.07	0.42*	0.27	-0.10	0.47*	0.47*	-0.01	0.61*	-0.17	0.20
IS 2508				1.00	0.28	-0.07	0.43*	0.56*	0.06	0.42*	0.65*	0.02	0.66*	0.02	0.25
IS 36563					1.00	0.41*	0.10	0.39*	0.30	0.20	0.27	0.42*	0.12	0.62*	0.34*
IS 6928						1.00	-0.07	0.17	0.41*	0.08	0.03	0.45*	-0.08	0.54	0.13
IS 854							1.00	0.52*	-0.03	0.77*	0.41*	-0.01	0.61*	-0.01	0.19
IS 1006								1.00	0.18	0.43*	0.56*	0.16	0.49*	0.36	0.47
IS 6958									1.00	-0.04	0.03	0.30	-0.01	0.54*	0.12
IS 12467										1.00	0.43*	0.03	0.63*	0.01	0.19
IS 17141											1.00	-0.04	0.65*	0.05	0.25
IS 18758												1.00	-0.08	0.50*	0.17
IS 18760													1.00	-0.09	0.25
ICSV 247-R														1.00	0.19
IS 3089 (S)															1.00

*Significant at $P<0.0001$.

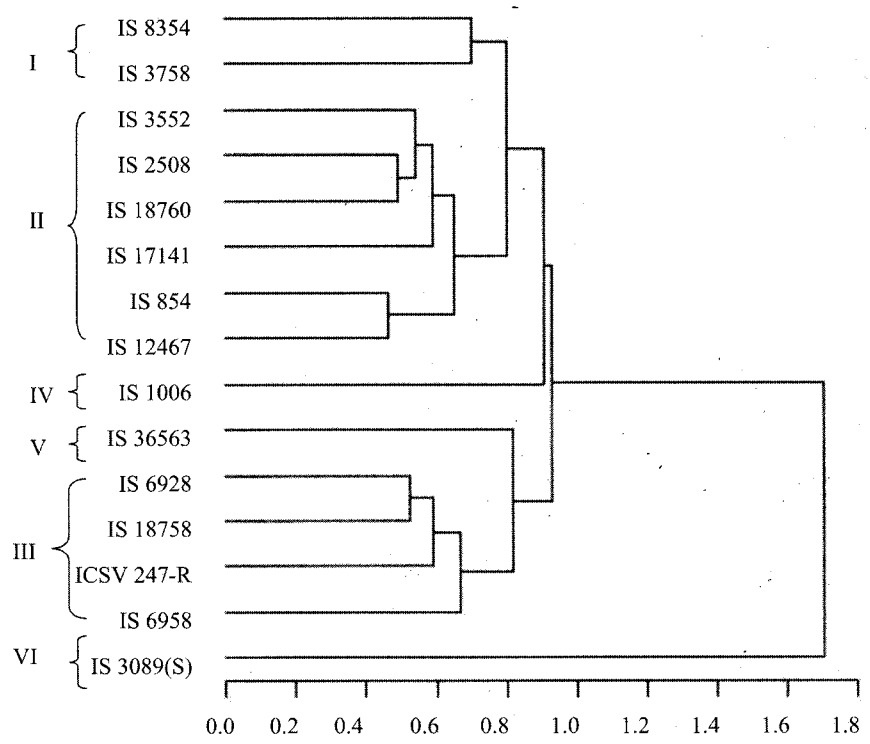

Fig. 1. Dendrogram showing groupings of the 15 tested sorghum lines based on their responses to anthracnose over 4-7 years (1992-1998) and across 14 geographical locations, based on cluster analysis

probably possess different resistance genes, and that the structures of pathogen populations, in term of virulence genes, varied across different geographical locations and over years although the possibility that the different lines could also respond differentially to different environmental conditions cannot be excluded (Kulkarni and Chopra, 1982).

Significant effects of location and year suggested that the weather conditions were more conducive to the disease at some locations over others, and varied over years. However, the relative effects of the weather were minimized by the artificial inoculation and sprinkler irrigation provided at some locations and seasons. Thus, the differences in location and year could be also due to the existence of variable pathogen populations at these locations. At all locations, anthracnose severity was high on the susceptible line IS 3089(S) indicating adequate disease pressure. Some locations, such as Pantnagar in India, Bagauda in Nigeria and Mansa in Zambia, had much higher average anthracnose severity on almost all tested sorghum lines over the 4-7 years than other locations. In contrast, average anthracnose severity was the lowest at Dharwad, Indore and Bangkok. Foliar anthracnose development is highly influenced by the weather factors, such as relative humidity and temperature, and thus the detailed analysis of weather data over many years in relation to progressive disease severity scores at each location would be needed to better understand how these factors affected foliar anthracnose development on sorghum lines. Our experience shows that obtaining the detailed weather data and disease scores at various growth stages of the crop has been a major limitation for a multilocation, multiyear nursery like this. However, from this study it would be easy to pick up few locations for the detailed epidemiological studies.

Variable reactions of sorghum lines to foliar anthracnose has been recorded in several studies reviewed by Mathur *et al.* (2002) and this is mainly due to the pathogenic variation in the *C. graminicola* populations, which in turn could be due to genetic mutation or host-directed virulence selection in the pathogen populations (Vanderplank, 1984).

The significant positively correlated severity levels on some tested lines suggested that those

lines may probably possess similar resistance gene(s), and therefore, varied similarly over time and locations as reported in pearl millet-*S. graminicola* system by Thakur *et al.* (2004). It could also be because they were affected by some shared factors, such as humidity, precipitation, etc. The cluster analysis demonstrated further that the 15 tested sorghum lines could be grouped into different groups based on their responses to anthracnose across different locations and over years. This analysis also provided very useful information for the future research on the genetic background of the resistance, and to breeding for more stable resistance. Some tested lines such as IS 2508 (Kafir caudatum from USA) and IS 18760 (Durra caudatum from USA); IS 854 (Kafir caudatum from USA) and IS 12467 (Caudatum from Sudan); or IS 6928 (Kafir caudatum from Sudan) and IS 18758 (Guinea caudatum from Ethiopia) may share similar genetic background and hence responded to *C. graminicola* similarly, and were placed closely within the same group. In contrast, lines such as IS 12467 (Caudatum from Sudan) and IS 6928 (Kafir caudatum from Sudan) that exhibited similar overall levels of resistance showed varying resistance pattern across environments and over years and thus grouped into distant groups, may possess different resistance genes. These results point out the prevalence of anthracnose resistance genes in the primary center of origin of sorghum (Ethiopia and Sudan) where maximum diversity in the crop and pathogen is expected to occur.

This study identified sorghum lines IS 18758, IS 12467 and IS 6928 as highly resistant, and IS 2508, IS 3552, IS 18760 and IS 6958 as moderately resistant across multiple locations and years, exhibiting high stability, and thus could be ideal sources of resistance for utilization in breeding programs. Furthermore, the responses of IS 12467 and IS 18758 varied differently, therefore, may be used as good resistance sources in breeding programs to integrate different resistance genes. These lines could also be employed alternatively over time or across space to avoid a quick breakdown of resistance. Several other lines that were stable at specific locations could be utilized in resistance breeding at those locations.

Identification and characterization of resistance genes and development of near-isogenic lines will be very useful for monitoring virulence change in *C. graminicola*. Characterization of pathogen populations for genetic structure and virulence pattern using molecular tools could be much more efficient and faster, therefore real-time monitoring the variation of virulence genes in *C. graminicola* populations may one day become achievable. This would help resistance breeding and strategic deployment of resistance to manage this disease.

ACKNOWLEDGMENT

We like to thank the Coordinator, All India Sorghum Improvement Project, Indian Council of Agricultural Research, New Delhi for his interest and support of this project. We duly acknowledge the contributions of collaborating scientists D.E. Hess, ICRISAT, Mali; S.C. Gupta, ICRISAT, Nigeria; G. Tegegne, Ethiopia; S.B. King, ICRISAT, Kenya; I. Iamsupasit, Thailand and G.M. Kaula, Zambia for conducting the nursery and providing the data used in this manuscript. We also thank B.V.S. Reddy, ICRISAT, Patancheru for his critical review of the manuscript.

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Received for publication June 13, 2006